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The impact of cow nutrient status during the second and third trimesters on age at puberty, antral follicle count, and fertility of daughters ☆

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ABSTRACT

Fluctuating feed resources to beef cows across the production cycle is a proven method for decreasing input costs; however, limiting nutrients during late gestation have been demonstrated to decrease ovarian follicle numbers in female offspring in some studies. We hypothesize that limiting nutrients to mature (≥ 3 yr) crossbred beef cows during the second and third trimesters would result in daughters that would have decreased follicle numbers detectable by ultrasonography as yearlings. Over four breeding seasons, pregnant beef cows ($n=397$) were assigned to either Low (**L**), Moderate (**M**) or High (**H**) nutrient intake during the second or third trimester, resulting in four dietary treatment groups (**L–H**, **L–L**, **M–H**, and **M–M**). Heifers ($n=416$) born to these cows were weighed at weaning and moved to a dry lot where they were monitored for behavioral estrus with the aid of heat detection patches. Two weeks before their first breeding season, heifers were submitted for ultrasonographic examination of their ovaries to determine antral follicle numbers. Heifers were placed with bulls for 60 d and pregnancy status was determined 45 d after the bulls were removed. Growth and reproductive traits were analyzed using the MIXED Procedure of SAS with maternal diet and year as fixed effects. Maternal dietary intake did not affect heifer growth rates, age at puberty, or antral follicle counts ($P \geq 0.40$). However, an increased proportion of the heifers born to dams fed a high nutrient diet during the third trimester (**L–H** or **M–H**) calved in the first 21 d of their first calving season ($P=0.004$). Antral follicle counts detectable by ultrasonography at yearling pre-breeding examination were greater in heifers that calved during the first 21 d of their first calving season ($P=0.02$); however, these heifers did not differ in age at puberty ($P=0.60$). From this study, we conclude that: (1) limiting nutrient intake during late gestation in mature (≥ 3 yr) beef cows does not influence the ovarian reserve or reproductive performance of daughters; (2) increasing maternal nutrient intake during

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the third trimester can improve the first service conception rates of daughters; and (3) pre-breeding ultrasonography to determine antral follicle counts is a good indicator of fertility for choosing replacement heifers.

1. Introduction

Replacing cows in the herd is a major cost associated with beef production (Clark et al., 2005; Mathews and Short, 2001), because high female replacement rates reduce the number of calves sold and the amount of genetic selection pressure that can be applied. Freetly et al. (2005) reported that nutrient intake could be limited for pregnant cows during the second trimester without altering the subsequent reproductive performance of the cows. However, maternal nutrient status during pregnancy may also affect the lifetime productivity of the female offspring, because there is evidence that both nutrient restriction and nutrient excess during pregnancy may negatively impact the ovarian reserve of the subsequent generation (Da Silva et al., 2002, 2003; Ireland et al., 2011; Sullivan et al., 2009).

The daughters of heifers that were fed a diet that was high in protein during the second trimester had a lower number of ovarian follicles by histological evaluation at 23 months of age (Sullivan et al., 2009). Furthermore, Ireland et al. (2011) reported that heifers restricted to 60% of their maintenance requirements during the first trimester bore daughters that had lower numbers of ovarian follicles detectable by ultrasonography during the first year of life. There is also evidence that over-nutrition during fetal development may decrease reproductive potential. In late pregnancy, female fetuses from over-fed ewe lambs had fewer follicles in their ovaries than moderately fed ewe lambs (Da Silva et al., 2002, 2003).

Increasing the nutrient status of the dam during the third trimester may have beneficial effects on the reproductive capacity of the daughters as well. Martin et al. (2007) reported that an increased proportion of the daughters born to dams provided a protein supplement during the third trimester calved in the first 21 d of their first calving season. Heifers that calve early at 2 yr of age have improved reproductive performance and wean heavier calves (Cushman et al., 2013a, 2013b; Funston et al., 2012; Lesmeister et al., 1973). Therefore, the current study was designed to test the hypothesis that nutrient status of mature beef cows (≥ 3 yr) during the second and third trimesters would influence the reproductive development and fertility of their daughters.

2. Materials and methods

All procedures were approved by the U.S. Meat Animal Research Center Animal Care and Use Committee.

2.1. Nutrient management of pregnant base cows

Three hundred and ninety-seven lactating composite beef cows (MARC III = ¼ Angus, ¼ Hereford, ¼ Pinzgauer, and ¼ Red Poll) ranging from 3 to 10 yr in age and determined to be pregnant by ultrasonographic examination were used across 4 yr. Cows remained on the study as long as they remained in the production herd and were determined to be pregnant. Cows were rotated among nutritional treatments during the years that they were on the study so that they did not repeat the same nutritional treatment while on study.

Gestational treatments consisted of four nutrient strategies based on previous results from our laboratory (Freetly et al., 2005). All cows were fed 100% of maintenance during the first trimester. The four experimental diets were composed of Low (**L**) or Moderate (**M**) nutrient levels during the second trimester and Low (**L**), Moderate (**M**), or High (**H**) nutrient levels during the third trimester of gestation. The Moderate nutrient diet was calculated to be 100% of maintenance, while the Low nutrient diet was 75% of maintenance and the High nutrient diet was 125% of maintenance.

Diets consisted of 67.3% corn silage, 27% chopped alfalfa hay, 5.5% corn, and 0.2% sodium chloride on a dry matter bases. On a dry matter basis, the diet had a CP of 11.3% and ME of 2.3 Mcal/kg. Diets stayed the same across treatments but the amount of feed was adjusted to provide different levels of metabolizable energy offered (Freetly et al., 2005). Metabolizable energy offered was determined by summing allocations for maintenance (MEm) and for pregnancy (MEy). All cows received an equal allocation for pregnancy but allocations for maintenance varied.

$$\mathrm{MEy} = \frac{40(0.4504 - 0.000766t)e^{(0.03233 - 0.0000275t)t}}{1000}$$

where t = day pregnant (NRC, 1996).

$\mathrm{MEm} = A \cdot (\mathrm{BW_{kg}})^{0.75}$ where A is 0.100 for Low intake, 0.135 for Moderate intake, and 0.170 for High intake, and BW is body weight at ultrasound determination of pregnancy. Cows were weighed and evaluated for body condition score at the start of the study, at the start of the third trimester, and just before the start of calving.

Cows within each treatment were maintained in one pasture each year with 50 cows per treatment each year. Because cows were on the study for 1–4 yr as long as they were pregnant at diagnosis, this only resulted in a total of three hundred and ninety-seven cows being used over the course of the study, as stated previously. Only 50% of the cows would be expected produce daughters for evaluation in the present study, and it was planned that we would produce 400 daughters. In fact, 416 daughters were produced, and this is just the deviation from the expected. Pastures were composed of smooth brome grass, and during the first half of the second trimester, 20% of intake was assumed to come from forage and 80% of intake was provided. Pastures were considered to be dormant from the middle of the second trimester through the third trimester.

2.2. Management of heifer progeny and data collection

Heifers ($n=416$) born to these cows were weighed at birth and again at weaning. At weaning, heifers were moved to the feedlot and fed to achieve a body weight of 330 kg at the start of breeding. Heifers were allowed ad libitum access to a diet that consisted of 35% chopped alfalfa hay, 64.8% corn silage, and 0.2% sodium chloride on a dry matter bases. Body weights were determined every 28 d. Beginning on November 1 (approximately 7 months of age in this production system), heifers were monitored for behavioral estrus with the aid of EstroTect™ patches. Patches were read daily and replaced every 14 d as required. After a heifer had two positive patches within 18 to 23 d of each other, her patch was not replaced. Approximately 2 weeks before the start of breeding, heifers were submitted for ultrasonographic examination to determine the location and numbers of all CL and location and number of all Small (3 to 5 mm), Medium (5.1 to 10 mm), and Large (>10 mm) follicles (Cushman et al., 2009).

Heifers were placed in a single herd and multi-sire mated to MARC III bulls during a 60-d breeding season. Ultrasonographic examinations to determine pregnancy status were performed 45 d after the end of the breeding season. For heifers diagnosed pregnant at ultrasonographic examination, fetal age was estimated based on size of the image and presence or absence of placentomes (Lamb et al., 2003). At birth, calf gender and body weight were recorded and bull calves were castrated.

2.3. Statistical analysis

For cows, data were analyzed with the pasture as the experimental unit. Reproductive and weight traits were analyzed using the MIXED Procedure of SAS with maternal diet and year of the study as fixed effects. For heifers, data were analyzed with the pasture that the dam was in for the last two trimesters as the experimental unit. Growth and reproductive traits were analyzed using the MIXED Procedure of SAS with year of the study and maternal diet as fixed effects and pasture as a random effect. First service conception rates were analyzed using the GLIMMIX procedure of SAS with year of the study and maternal diet as fixed effects and pasture as a random effect.

To examine individual heifer performance and performance based on calving group, heifer was used as the experimental unit. The CORR procedure of SAS was used to examine the associations between reproductive traits and growth traits for the individual heifers. Additionally, the heifers that produced a calf were grouped into 21 d calving periods (Cushman et al., 2013a; Funston et al., 2012). In these analyses, reproductive and growth traits were analyzed using the MIXED procedure of SAS with treatment and calving period as the fixed effects. In this case, treatment was kept in the model to partition any effects due to maternal nutrition, but calving group could not be assigned by the pasture of the dam during the last two trimesters. This necessitated the use of heifer as the experimental unit for these analyses,

3. Results

3.1. Cows

Pregnant cows did not differ in age or body weight when diets were initiated (Table 1; $P \geq 0.91$). By the start of the third trimester, cows that had been held to the low nutrient diet during the second trimester (**L–H** and **L–L**) were lighter than cows provided the moderate nutrient

Table 1
Influence of changes in maternal diet during the second and third trimesters on cow performance during the second and third trimesters of pregnancy and in the next breeding season.

Trait	Maternal nutrition[a]				P-value
	L–H	L–L	M–H	M–M	
n	4	4	4	4	-
Lactating cows	241	244	240	248	-
Age, y	5.9 ± 0.3	5.8 ± 0.3	5.8 ± 0.3	5.7 ± 0.3	0.96
Initial BW, kg	602.6 ± 5.7	606.6 ± 5.7	605.4 ± 5.7	601.4 ± 5.7	0.91
Initial BCS	5.8 ± 0.1	5.9 ± 0.1	5.9 ± 0.1	5.9 ± 0.1	0.93
3rd trimester BW[b], kg	578.1 ± 16.8[f]	579.0 ± 16.8[f]	633.7 ± 16.8[g]	631.4 ± 16.8[g]	0.05
3rd trimester BCS[b]	5.6 ± 0.1[f]	5.7 ± 0.1[f]	6.0 ± 0.1[g]	6.1 ± 0.1[g]	0.04
Calving BW[c], kg	663.0 ± 10.7[f]	623.0 ± 10.7[g]	691.5 ± 10.7[f]	674.7 ± 10.7[f]	0.005
Calving BCS[c]	6.0 ± 0.2[f]	5.5 ± 0.2[g]	6.2 ± 0.2[f]	6.0 ± 0.2[f]	0.04
Percent calving	93.7 ± 1.3	94.3 ± 1.3	97.1 ± 1.3	97.6 ± 1.3	0.12
Percent heifers	50.4 ± 2.4	42.6 ± 2.4	44.7 ± 2.4	44.8 ± 2.4	0.18
Percent re-bred[d]	90.4 ± 2.2	87.0 ± 2.2	89.8 ± 2.2	88.2 ± 2.2	0.71
Days to calving[e]	294.8 ± 1.1	295.3 ± 1.1	295.2 ± 1.1	295.3 ± 1.1	0.99

[a] L–H=Low–High, L–L=Low–Low, M–H=Moderate–High, and M–M=Moderate–Moderate nutrient intake.
[b] Body weight and body condition score at the start of the third trimester of pregnancy.
[c] Body weight and body condition score at the start of calving.
[d] Determined by ultrasonography 40 d after the end of the next breeding season.
[e] Days from the start of the next breeding season to calving.
[f] Within a row, means with different superscripts are different.
[g] Within a row, means with different superscripts are different.

diet during the second trimester ($P=0.05$). By calving, only those cows maintained on a low nutrient diet throughout the second and third trimesters (**L–L**) were lighter ($P=0.005$), while those fed a low nutrient diet during the second trimester and a high nutrient diet during the third trimester (**L–H**) were no longer different from the other treatment groups.

A similar pattern was observed with body condition scores. Initially there was no difference ($P=0.93$) in body condition scores; however, by the start of the third trimester, cows fed on a low nutrient diet (**L–H** and **L–L**) had lower body condition scores than cows fed a moderate nutrient diet (**M–H** and **M–M**) during the second trimester ($P=0.04$). By calving, only cows fed a low nutrient diet throughout the second and third trimesters (**L–L**) had reduced body condition scores compared to the other groups ($P=0.04$).

The percentage of pregnant cows that carried their calf to term and the percentage of heifer calves that were born did not differ among maternal nutrient groups ($P \geq 0.12$). Re-breeding performance of cows was not influenced by nutrient status during the second and third trimesters (Table 2), because there was no difference in the percent pregnant at ultrasound ($P=0.77$) or the number of days from being placed with the bulls until calving ($P=0.99$).

3.2. Heifers

Maternal nutrient status during the second and third trimesters did not influence heifer birth weight, pre-weaning ADG, or heifer weaning weight (Tables 2, $P \geq 0.40$). Furthermore there were no differences in weight at puberty, post-weaning ADG, or breeding weight ($P \geq 0.60$) due to maternal nutritional treatments. There was a significant negative correlation of pre-weaning ADG with age at puberty, such that heifers that gained more had an earlier age at puberty ($r=-0.19$, $P<0.0001$). There was no correlation of post-weaning ADG with age at puberty ($P=0.18$). Both pre-weaning ADG ($r=0.11$, $P=0.02$) and post-weaning ADG ($r=0.11$, $P=0.02$) had a significant positive correlation with antral follicle count at pre-breeding ultrasonographic examination.

Maternal nutrient status during the second and third trimesters did not influence the percent of heifers that had displayed behavioral estrus by the start of the breeding season or the age at puberty (Tables 3, $P \geq 0.60$). Antral follicle count determined by ultrasonography at pre-breeding examination did not differ among heifers due to the maternal nutritional treatments ($P=0.50$). Furthermore, the number of Medium (5.1 to 10 mm) and Large (> 10 mm) follicles did not differ among heifers due to maternal nutrient intake ($P>0.10$). While there was no difference in the percent of heifers that were pregnant after a 60 d breeding season ($P=0.23$), heifers that were born to dams that were fed an increased nutrient diet (**L–H** and **M–H**) during the third trimester tended to conceive earlier based on estimated fetal age at ultrasonographic determination of pregnancy status ($P=0.07$). Ultrasonographic results were confirmed by a decreased calving day ($P=0.07$), defined as the number of days from the start of the calving season to calving. As would be expected, this was due to a strong negative correlation between estimated fetal age at ultrasonography and days to calving ($r=-0.89$, $P<0.0001$), because fetuses that were estimated to be older at ultrasonography had a shorter number of interval from the start of the calving season to calving. Together, this resulted in an increased percentage of heifers that were calved in the first 21 d of the calving season in those heifers born to dams fed a high nutrient diet (**L–H** and **M–H**) during the third trimester ($P=0.004$).

Maternal nutrition during the second and third trimesters did not influence the birth weights of the calves produced in the second generation (Table 3; i.e. the grand-progeny of the cows on which the diets were imposed). There was no difference between maternal dietary treatments in the percentage of heifers born in the second generation. Although increased maternal nutrient status in the third trimester (**L–H** and **M–H**) increased the percentage of daughters calving in the first 21 d, it did not alter weaning weights of the calves in the second generation ($P=0.30$).

3.3. Calving periods

When daughters were grouped by their calving period, there were no differences in growth or weight traits (Table 4; $P \geq 0.21$) that could be used to identify heifers that would calve early in their first calving season. Age at puberty did not differ among the daughters that calved

Table 2
Weight and growth traits of heifers born to cows that differed in nutrient status during the second and third trimesters of pregnancy.

Trait	Maternal nutrition[a]				*P*-value
	L–H	L–L	M–H	M–M	
n	4	4	4	4	–
Heifers	111	99	99	107	–
Birth weight, kg	36.6 ± 0.7	37.3 ± 0.7	36.5 ± 0.7	38.0 ± 0.7	0.40
Pre-weaning ADG, kg/d	0.94 ± 0.01	0.95 ± 0.01	0.96 ± 0.01	0.96 ± 0.01	0.70
Weaning weight, kg	190.2 ± 2.7	191.3 ± 2.7	191.9 ± 2.7	194.3 ± 2.7	0.74
Weight at puberty, kg	311.5 ± 3.4	314.7 ± 3.4	315.8 ± 3.4	318.2 ± 3.4	0.60
Post-weaning ADG, kg/d	0.77 ± 0.01	0.76 ± 0.01	0.76 ± 0.01	0.76 ± 0.01	0.89
Breeding weight, kg	374.7 ± 4.6	375.2 ± 4.6	374.0 ± 4.6	377.7 ± 4.6	0.95

[a] L–H = Low–High, L–L = Low–Low, M–H = Moderate-High, and M–M = Moderate–Moderate nutrient intake.

Table 3
Reproductive traits of heifers born to cows that differed in nutrient status during the second and third trimesters of pregnancy.

Trait	Maternal nutrition[a]				*P*-value
	L–H	L–L	M–H	M–M	
n	4	4	4	4	–
Heifers	111	99	99	107	–
Percent pubertal[b]	96.4 ± 3.2	95.1 ± 3.2	92.0 ± 3.2	96.6 ± 3.2	0.73
Age at puberty, d	316.5 ± 4.1	312.4 ± 4.1	315.6 ± 4.1	320.5 ± 4.1	0.60
Antral follicle count[c]	22.8 ± 0.7	22.0 ± 0.7	22.6 ± 0.7	21.4 ± 0.7	0.50
Percent pregnant[d]	85.5 ± 2.1	89.9 ± 2.1	92.0 ± 2.1	88.5 ± 2.1	0.23
Fetal age[e], d	85.8 ± 1.5[g]	83.0 ± 1.5[h]	88.6 ± 1.5[g]	85.4 ± 1.5[h]	0.07
Calved, %	81.5 ± 2.1[g]	82.5 ± 2.1[g]	90.0 ± 2.1[h]	82.0 ± 2.1[g]	0.06
Calved first 21 d, %	51.5 ± 2.6[g]	42.0 ± 2.6[h]	55.1 ± 2.6[g]	40.3 ± 2.6[h]	0.004
Calving day[f]	22.7 ± 1.9[g]	27.1 ± 1.9[h]	21.1 ± 1.9[g]	24.1 ± 1.9[h]	0.07
Calf birth weight, kg	31.3 ± 0.6	32.2 ± 0.6	31.6 ± 0.6	31.2 ± 0.6	0.71
Percent heifers	48.3 ± 4.9	48.4 ± 4.9	41.0 ± 4.9	45.3 ± 4.9	0.69
Calf weaning weight, kg	176.5 ± 2.0	174.8 ± 2.0	180.1 ± 2.0	175.4 ± 2.0	0.30

[a] L–H = Low–High, L–L = Low–Low, M–H = Moderate–High, and M–M = Moderate–Moderate nutrient intake.
[b] Percent of the heifers that was pubertal by the start of the breeding season.
[c] Determined by ultrasonography at pre-breeding examination.
[d] Percent pregnant after a 60-d breeding season with multi-sire pasture natural service.
[e] Estimated fetal age based on ultrasonographic imaging (Lamb et al., 2003).
[f] Days from the start of the calving season to calving.
[g] Within a row, means with different superscripts are different.
[h] Within a row, means with different superscripts are different.

early (1–21 d), intermediate (22–43 d), or late (> 43 d) in their first calving season ($P=0.75$). However, antral follicle numbers detectable by ultrasonography at the pre-breeding examination (14 months) were greater in heifers that calved in the first 21 d of their first calving season ($P=0.02$). Birth weights of the calves born to these heifers increased as calving period increased ($P<0.0001$). The unadjusted weaning weights decreased as calving period increased ($P<0.0001$), due to the decrease in days from birth to weaning.

4. Discussion

The results of the present study do not support the hypothesis that maternal nutrient status of mature cows (≥ 3 yr) during the last two trimesters of gestation influences development of the ovarian reserve or age at puberty in female offspring. In contrast to other studies (Sullivan et al., 2009; Ireland et al., 2011), we observed no difference in the number of antral follicles detectable by ultrasonography at a pre-breeding examination of daughters at approximately 14 months of age. This could be because our restriction (75% of maintenance) was not nearly as severe as those imposed in previous studies, or because in the previous studies maternal nutrient status was altered during the first and second trimesters, while in the present study maternal nutrient status was altered during the second and third trimesters. The gonad is forming during the first trimester, and Mossa et al. (2013) clearly demonstrated impacts of under-nutrition to pregnant heifers during the first trimester on daughter follicle counts. However, Da Silva et al. (2002, 2003) reported a decrease in the number of follicles in the ovaries of female fetuses gestated in ewe lambs fed with a high nutrient diet during the third trimester. Therefore, it is more likely that the difference in the present study was due to less severe impacts because restriction was only 75% of maintenance, or to the use of mature cows as compared to heifers (Ireland et al., 2011; Sullivan et al., 2009) or ewe lambs (Da Silva et al., 2002, 2003) in previously published work. It can be logically hypothesized that these nutritional stresses during the second and third trimesters have a greater impact on young females that are still growing themselves during their first pregnancy than on mature females. How factors such as degree of nutrient restriction and timing of nutrient restriction are communicated to the developing fetus will need to be investigated further in the future.

As we have demonstrated previously (Freetly et al., 2005), reducing the nutrient status to the cows during the second or third trimester (**L–H** and **L–L**) did not negatively impact their re-breeding performance. In the previous study, cows were also maintained in a lower nutrient status during the postpartum period, and this did not negatively impact the percentage that had a CL detectable by ultrasonography at pre-breeding examination. Combined with the results of the present study, which demonstrated no differences in the percent pregnant or the days to calving, it can be concluded that reducing nutrient status of cows to 75% of maintenance during the second or third trimester does not negatively impact re-breeding performance and can be utilized to reduce maintenance costs for the cow herd during the winter months.

A greater proportion of daughters of cows fed a high nutrient diet during the third trimester (**L–H** and **M–H**) calved in the first 21 d of their first calving season than daughters of cows fed a low (**L–L**) or moderate (**M–M**) nutrient diet in the third trimester. Other studies have demonstrated impacts of nutrient intake during the third trimester on daughter reproductive performance. Martin et al. (2007) reported that a greater proportion of heifers

Table 4
Growth and reproductive traits for heifers based on calving periods during their first calving season.

	Calving period[a]			*P*-value
	1	**2**	**3**	
Heifers	197	99	54	–
Birth weight, kg	36.9 ± 0.4	37.1 ± 0.5	37.0 ± 0.7	0.24
Pre-weaning ADG, kg/d	0.95 ± 0.01	0.93 ± 0.01	0.95 ± 0.01	0.45
Weaning weight	192.8 ± 1.5	188.2 ± 2.1	190.7 ± 2.9	0.21
Weight at puberty	313.1 ± 2.9	313.1 ± 4.1	319.0 ± 5.7	0.63
Post-weaning ADG, kg/d	0.76 ± 0.01	0.77 ± 0.01	0.77 ± 0.01	0.41
Breeding weight, kg	375.4 ± 2.5	373.2 ± 3.5	375.4 ± 7.4	0.86
Age at puberty, d	316.0 ± 2.9	319.3 ± 4.1	314.7 ± 5.8	0.75
Antral follicle count[b]	23.0 ± 0.5[c]	21.0 ± 0.8[d]	20.2 ± 1.0[d]	0.02
Calf birth weight, kg	35.8 ± 1.4[c]	37.1 ± 1.4[d]	38.4 ± 1.5[e]	< 0.0001
Calf weaning weight, kg	201.3 ± 8.0[c]	184.1 ± 8.3[d]	161.4 ± 8.6[e]	< 0.0001

[a] 1 = heifers that gave birth on days 1–21 of their first calving season, 2 = heifers that gave birth on days 22–42 of their first calving season, and 3 = heifers that gave birth on or after day 43 of their first calving season.
[b] Determined by ultrasonography at pre-breeding examination.
[c] Within a row, means with different superscripts are different.
[d] Within a row, means with different superscripts are different.
[e] Within a row, means with different superscripts are different.

born to cows provided with 0.45 kg/d of protein supplement during the third trimester calved in the first 21 d of their first calving season. Excess protein during gestation can negatively impact the ovarian reserve; however, while fed to exceed requirements, the amount of protein fed in the current study was not nearly as extreme as previously reported (Sullivan et al., 2009). Martin et al. (2007) further reported no influence of maternal protein supplementation on age at puberty of the daughters. Combined with a lack of difference in the number of antral follicles detectable by ultrasonography at 14 months of age in the present study, this could indicate that the increased proportion of heifers calving in the first 21 d is due to changes in adiposity (Micke et al., 2011) or altered uterine function. Clearly, the increased proportion of heifers calving in the first 21 d was not due to greater rates of growth, decreased age at puberty, or a greater number of antral follicles.

A novel finding in this study was that heifers that calved in the first 21 d of their first calving season had greater numbers of antral follicles detectable by ultrasonography at 14 months of age. Antral follicle count has been reported as an indicator of fertility in heifers and cows in a numbers of studies (Cushman et al., 2009; Mossa et al., 2012; Tessaro et al., 2011); however, there have also been studies where antral follicle count did not reflect fertility in cattle (Snelling et al., 2012; Starbuck-Clemmer et al., 2007). Mossa et al. (2012) reported a tendency for dairy cows with low follicle numbers to have an increased number of services per conception and lower pregnancy rates in a seasonal production system. Likewise, Repeat Breeder cows that failed to conceive in two consecutive seasons were older at first calving and had fewer antral follicles at slaughter (Cushman et al., 2013b; Maurer and Echternkamp, 1985). Given the similar relationship in the current study, it may be that lower follicle numbers are associated with delayed conception and in production systems where seasonal breeding is used, this delay in conception in some years can lead to a decrease in overall pregnancy rates while in other years it simply results in a delay in conception.

Birth weights of the calves increased as calving period increased. This is in agreement with Funston et al. (2012) and Cushman et al. (2013a). The reason for this increase in birth weight is unclear. Since actual breeding dates are unknown it could be related to an increase in gestation length that resulted in heavier birth weights, but there is no way to confirm the gestation length of these animals because they were bred by natural service in a pasture situation with no observation of mating behavior.

Although the calves born early were lighter, they had a greater unadjusted weaning weight due to the increased number of days between birth and the common weaning date. Cushman et al. (2013a) reported that this increase in weaning weight continued for 6 parturitions. Therefore, methods to identify replacement heifers that will conceive early in their first breeding season are of great economic benefit to the cow calf producer. As such, identifying heifers with high antral follicle numbers by an ultrasound-based reproductive tract evaluation prior to the first breeding season may aid in selecting the replacement heifers with the greatest potential to calve early and be highly productive.

5. Conclusion

In conclusion, there were no negative effects of reducing nutrient intake by 25% in mature lactating cows ($\geq$3 yr) during the second and third trimesters on daughter growth or reproductive performance as heifers, most likely because cows are less susceptible to this challenge than growing heifers. If reducing nutrient intake in pregnant cows does impact the ovarian reserve of their daughters (Ireland et al., 2011; Sullivan et al., 2009), it must be when nutrient restrictions are greater than those applied during this feeding regimen (25%). Increasing nutrient intake to the dam during the third trimester increased the proportion of daughters that calved in the first 21 d of their first calving season by mechanism that remain unclear and most likely do not involve changes in the ovarian reserve or age at puberty.

Conflict of interest statement

We declare that there is no conflict of interest in the publication of this paper.

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